Reflections on the genus in ornithology

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In the biologist's every day life, the use of a genus name is inevitable if not compulsory. Whether he studies the protozoan *Entamoeba*, the mosquitoes *Culex* or *Anopheles*, the herring *Clupea*, the Great Tit *Parus* or man himself *Homo*, for him the genus-name is significant if not decisive. He rarely ponders on what a genus actually means as a concept in systematic biology. Indeed, in most instances this is of no relevance to him. However, he may suddenly become painfully aware of it when taxonomists start to arrange the species of his study according to revised ideas of generic grouping. Worse still, he may see the familiar genus-name changed.

Almost 30 years ago I tried to formulate my thoughts on the essence of the genus in a Dutch journal (Voous 1964). Some time later I explained these in another paper written in English (Voous 1975), adding remarks on the theoretical and practical limits of genera in the warblers *Acrocephalus* and *Hippolais*, the gulls *Larus* and terns *Sterna*, and the geese *Anser* and *Branta*. The main conclusions were that, in contrast to species, genera have no reality in nature, that genera should be defined pragmatically and that non-taxonomic biologists are primarily interested in genus-names rather than in the genus itself. *Mutatis mutandis* this would apply to all other systematic categories above the species level. Only at the higher end, towards the category of the phylum, diversity in ontogeny and structure shows differences in principle rather than degree.

Introductory considerations

Renewed interest in the genus was induced by the publication of 2 important ornithological works, both of which have made important and markedly bold attempts to group the species of the birds of the world according to modern views and methods: Hans E. Wolters (†1991), *Die Vogelarten der Erde* (1975–1982), and Charles G. Sibley & B.L. Monroe, Jr., *Distribution and Taxonomy of Birds of the World* (1990).

Wolters announced himself as a strict follower of W. Hennig's phylogenetic systematics (Hennig 1950, 1966). Sibley & Monroe, though also following Hennig's principles of cladistic analysis, constructed a gigantic new building of bird systematics, based on the corner stones of DNA-studies. As was to be expected, Wolters's and Sibley & Monroe's classifications are as different *inter se* as each of these is from the traditional Wetmore system and its modifications.

Though of little relevance here, I have always had my own serious doubts as to the significance of Hennigian methods in taxonomy (Voous 1980, concurred with by Mayr 1982; 226–233). Whether viewed as a branching tree up to the finest twigs and end buds, or as a pruned bunch of grapes in which the pruning is executed by all natural phenomena in existence, the growth of certain twigs or grapes are favoured, while others

lead to extinction or radical pruning. The result is that the tree of life formed by both transient and recent species is far too complicated and too incompletely known, if known at all, so that the recognition of branching points, as required by Hennig, involves too many basic uncertainties as to be of any real help in understanding the road of evolution. When making a choice out of a multitude of possible options for the reconstruction of a phylogenetic tree, the word "parsimonious" emerges as of having magical power. I must confess that, English not being my mother's tongue, I have met this word only in Hennigian contexts and I am not impressed by it. As every experienced biologist knows, nature's ways are, and probably always have been, more capricious and unpredictable than man can encompass. Hence, all Hennigian-derived phylogenetic trees are theories, not necessarily better or nearer to reality than any other serious endeavour to reconstruct the past. Trying to discriminate between 'apomorphic', 'plesiomorphic' and other categories of characters, which is another important item in Hennigian methodology, is as subjective a procedure as it was to distinguish between homologous and analogous characters or structures in old-fashioned comparative anatomy, which therefore ultimately failed.

With this in mind and passing by the several published theoretical observations on the genus concept, I have ventured to evaluate the use of genera in the comprehensive works of Wolters (1975–1982) and Sibley & Monroe (1990). The results of the evaluation will be compared with the conclusions arrived at in earlier papers (Voous 1964, 1975).

Comparing the uses made of genera in avifaunal lists

In order to evaluate the genus concepts adhered to by Wolters (1975–1982) and Sibley & Monroe (1990) I have compared the genus-names accepted in these works with those used in:

(1) New World breeding birds, as in the A.O.U. *Check-list of North American Birds* (6th ed., 1983): Nearctic region only.

(2) Old World breeding birds, as in the *List of Recent Holarctic Bird Species* (Voous 1973, 1977): Europe only.

(3) Tropical Asiatic birds, as in *The Birds of Sumatra* (van Marle & Voous 1988): breeding birds of Sumatra and satellite islands.

As stated before, Wolters has tried to apply cladistic methods at every taxonomic level, including that of subgenera. Hence his classification differs from that of any of his predecessors. The actual reasoning behind each individual case is not explained, but the reader is referred to an earlier paper on the limits of genera in ornithology in general (Wolters 1971). As a result Wolters lists no less than 356 (289) genera in North America, 270 (213) genera in Europe, and 281 (220) genera in Sumatra (traditional numbers added in parentheses).

In contrast, Sibley & Monroe have been wise enough to lay the stress on their truly revolutionary arrangement and sequence of higher taxonomic categories, viz. tribe, family, infraorder, suborder, order, parvclass, infraclass, subclass. They have rarely deviated from the traditional path in the extent and limits of genera and the use of genus-names. This is all the more pleasurable since the names and their meaning in taxonomy will

be recognised by ornithologists and biologsts of any discipline. Actually, their basically quantitative biochemical methods would have hardly left them room for deciding otherwise. Sibley & Monroe list 291 (289) genera in North America, 212 (213) genera in Europe, and 226 (220) genera in Sumatra (traditional numbers added in parentheses).

Fortunately, Wolters and Sibley & Monroe concur in as many as 24 instances, listed below, in which they deviate from one or more of the traditional classifications with which their works were compared:

Morus (not *Sula*) *bassanus*

Ixobrychus (not *Dupetor*) *flavicollis*
Nyctanassa (not *Nycticorax*) *violacea*
Casmerodius (not *Egretta*) *albus*
Mergellus (not *Mergus*) *albellus*

Asturina (not *Buteo*) *nitida*

Porphyrio (not *Porphyrula*) *martinica*
Burhinus (not *Esacus*) *magnirostris*
Eudromias (not *Charadrius*) *morinellus*
Micropalama (not *Calidris*) *himantopus*
Steganopus (not *Phalaropus*) *tricolor*
Larus (not *Xema*) *sabini*

Rhaphidura (not *Chaetura*) *leucopygialis*
Tachymarptis (not *Apus*) *melba*
Todiramphus (not *Halcyon*) *chloris*

Actenoides (not *Halcyon*) *concretus*
Tricholestes (not *Hypsipetes*) *criniger*
Iole olivacea (not *Hypsipetes charlottae*)
Ixos (not *Hypsipetes*) *malaccensis*

Hemixos (not *Hypsipetes*) *flavala*
Eumyias (not *Muscicapa*) *thalassima*
Eumyias (not *Muscicapa*) *indigo*

Psilorhinus (not *Cyanocorax*) *morio*

Hesperiphona (not *Coccothraustes*) *vespertina*

Case studies

Anatidae: swans, geese, ducks

The number of genera recognized by Wolters is 72, by Sibley & Monroe 44, average number of species per genus 2 and 4, respectively. Recognising 13 genera of surface-feeding or dabbling or paddling ducks by Wolters, instead of the one genus *Anas* by Sibley & Monroe, means in terms of cladistic analysis that Wolters's first genus, "*Melananas*" for the African Black Duck *Anas sparsa*, is the 'sister-group' of all following genera combined. It is hard to believe that evidence in favour of this suggestion is available, nor that the 3 species of wigeon '*Mareca*', following '*Melananas*' have subsequently together branched off from the main and only stem from which in later times all other *Anas*-ducks have derived. The scholarly ecological studies by Johnsgard (1965) on which Voous (1973) and others have based their sequence of ducks, would not suffice for that purpose, as nothing is known of the real history of the evolution of these ducks.

Curiously enough, the delimitation of these duck-genera by Wolters conforms almost exactly with the genera recognised in older European works and perpetuated still in the 4th edition of the A.O.U. *Check-list*

of North-American Birds (1931) in which *Anas* is split into 9 genera: *Anas, Chaulelasmus, Dafila, Paecilonetta, Eunetta, Nettion, Querquedula, Mareca* and *Spatula*. Morphological differences (e.g. in the structure of the bill, corresponding with feeding habits and habitats) formed the background for recognising these groups as genera. So we are back to where taxonomy started: comparative morphology, as a subjective, but verifiable basis for genus-recognition, now in modern Hennigian disguise. Realising that this is the position of a modern classification does not mean yielding to scientific incapacity, but is merely to put the record straight.

Using 50 (Wolters) or 35 (Sibley & Monroe) genera for all 40–42 duck species together, signifies differences in taxonomic view and treatment, but one method is scientifically not more acceptable than the other. For the general ornithologist, however, a restricted number of genus-names reflects the situation more clearly that the similarity of duck species in appearance and behaviour is more apparent than the difference. Besides, in spite of differences in male breeding attire, these birds are genetically remarkably closely related as testified by the occurrence of the most extravagant, and often fertile, hybrid combinations, occurring as well in captivity as in nature; and was it not the possibility of producing fertile hybrids that was considered the crucial condition for recognising "wide" genera in Wolters's earlier writings (Wolters 1949, 1950)?

Falconidae: falcons

The number of genera of falcons recognised by Wolters is 10, by Sibley & Monroe one, average number of species per genus 4 and 39, respectively. Admittedly, there are marked differences between the 'inoffensive' kestrels '*Tinnunculus*' and the 'fierce' gyrfalcons and peregrines '*Hierofalco*'. If the use of the one genus-name *Falco* for all falcons is considered unsatisfactory because of the differences between the extremes, the splitting up of the genus could be considered a remedy. This would leave Merlin '*Aesalon*', Hobby '*Falco*' and Eleonora's Falcon '*Falco*' in intermediate positions and would place the Red-footed Falcon '*Erythropus*' on a specialised side-branch. Still, the history of the evolution of falcons is virtually unknown. For the use of a variety of genus-names for the falcons, nothing but the old-fashioned method of weighted phenological taxonomy remains in stock. Trying to find 'sister-groups' in this and comparable cases is unrealistic, and Hennigian methods fail or are at best as subjective as any other method.

Calidridinae (*Eroliinae*): *sandpipers*

The number of genera recognised by Wolters is 11, by Sibley & Monroe 6, average number of species per genus 2 and 4, respectively. Basically the same considerations as in the case of the *Anas*-ducks could apply to the use of genus-names in this group of waders which, as in ducks, look so much alike and behave so similarly *inter se*, yet in some respects can be so markedly different. Subjective comparative morphology rather than the reconstruction of branching points in their long line of evolution has provided the basis for the recognition of the genera *Calidris* (Knot), *Erolia* (Curlew Sandpiper), *Heteropygia* (Pectoral Sandpiper), *Ereunetes*

(Semipalmated Sandpiper), *Crocethia* (Sanderling), *Pelidna* (Dunlin), *Arquatella* (Purple Sandpiper). They are distinguishable mainly on account of one or two vestigial webs at the base of toes and the absence, presence or size of the hind toe, none of which characters seem to play a major specific role in sandpipers' lives. Apart from weak scientific evidence, a profusion of genus-names more likely conceals than elucidates the degrees of relationship in these waders.

Laridae: gulls

The number of genera of gulls recognised by Wolters is 12, by Sibley 6, average number of species per genus 4 and 8, respectively. In a former paper (Voous 1975) I have tried to show that a wide genus *Larus*, including such extremes as the Great Black-backed Gull *Larus marinus* and Little Gull *Larus minutus* is consistent with the facts only when in the related terns a similarly wide genus concept is accepted. It was therefore proposed to list the Caspian Tern (*caspia*) and the Little Tern (*albifrons*) and all terns in between as members of one genus *Sterna*. The alternative view is to have these 2 genera divided into several, which is what Wolters has done. Apart from the Kittiwake *Rissa* and the Ivory Gull *Pagophila*, all 'white-headed' gulls, from Common Gull (*canus*) to Great Black-backed (*marinus*) and Glaucous (*hyperboreus*) Gulls are listed by Wolters as *Larus*, as opposed to the "hooded' gulls, which are arranged in as many as 7 genera: *Adelarus* (Hemprich's or Aden Gull, 2 species), *Ichthyaetus* (Great Black-headed Gull, 1 species), *Chroicocephalus* (Black-headed Gull, 13 species), *Atricilla* (Laughing Gull, 3 species), *Hydrocoelus* (Little Gull, 1 species), *Rhodostethia* (Ross's Gull, 1 species) and *Xema* (Sabine's Gull, 2 species). Even a detailed cladistic background for this classification cannot provide the real evolutionary history which has brought about the present wealth of gull species, disclosing the subjective nature of this arrangement. Apart from that, the question remains whether one considers it more practical and helpful to adhere to one, well-defined large genus or alternatively should accept a number of less clearly defined smaller genera. Obviously, most present authors opt for the least amount of genus splitting.

Concluding remarks

The practicability and direct understanding of the limits of genera and of genus-names are the most relevant, and at the same time most widely appreciated, requirements for the genus, at least in ornithology. Most authors agree on the fact that whenever possible the genus should include a monophyletic group of species distinct from other such monophyletic groups. In most cases, in the absence of palaeontological data, the reality of a monophyletic origin of an individual genus cannot be or has not yet been proved. Hennigian analysis has not improved this situation. Real though the clustering of species is in evolutionary history, the reality and even the meaning of genus-limits are questionable. Genus-names remain as auxiliary help for understanding and memorising classification systems and in this respect are useful for any kind of ornithological research. Pragmatic rather than scientific values should be attached to bird genera and their naming.

In addition some of my earlier conclusions seem to have remained valid: (1) species, as functions of time and place, are a reality in nature; (2) genera are abstractions and as such do not exist in nature; (3) species can be discovered in nature, genera cannot; genera are invented (Voous 1964); (4) evolutionary development is gradual; in contrast, the distinction of genera is discontinuous by its very nature; (5) the recognition of genera should not be considered a necessary means of expressing evolutionary relationships, a presumption which after all is an unwelcome heritage of 19th century thinking; (6) "The choice in the use of [named] genera should be practised according to the same standards as [for] literary style and with the same . . . elegance and precision, combining the subtilities of art with the [rigid] abilities of science" (Voous 1975: 982).

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